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Molecular phylogenetic analysis of Punctoidea (Gastropoda, Stylommatophora)

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Abstract

A phylogenetic analysis using a combination of mitochondrial (COI, 16S) and nuclear markers (ITS2, 28S) indicated that Punctoidea, as previously interpreted, is polyphyletic. It comprises two main groups, containing northern hemisphere (Laurasian) and predominantly southern hemisphere (Gondwanan) taxa respectively, treated here as separate superfamilies. Within Punctoidea sensu stricto, Punctidae, Cystopeltidae and Endodontidae form separate monophyletic clades, but Charopidae, as currently interpreted, is paraphyletic. Most of the charopid taxa that we sequenced, including *Charopa coma* (Gray, 1843) and other Charopinae, grouped in a clade with Punctidae but some charopid taxa from Australia and South America grouped with Cystopeltidae. Cystopeltidae previously contained a single Australia-endemic genus, *Cystopelta* Tate, 1881, but our analysis suggests that it is considerably more diverse taxonomically and has a much wider distribution. For taxonomic stability, we suggest that Charopidae be retained as a family-level group for now, pending further study of the systematic relationships of its constituent taxa. A new superfamily, Discoidea, is erected here for two Northern Hemisphere families, Discidae and Oreohelicidae, which were previously assigned to Punctoidea. The North American species *Radiodomus abietum*, previously in Charopidae, is also here assigned to Discoidea. The phylogenetic relationships of Helicodiscidae, previously assigned to Punctoidea, were not fully resolved in our analysis, but the family is apparently closely related to Arionoidea Gray, 1840 and infraorder Limacoidei.

Key Words

Bayesian Inference, Discoidea, Helicodiscidae, land snails, maximum likelihood

Introduction

The Punctoidea Morse, 1864 is a group of stylommatophoran land snails that are typically of small to minute size. As interpreted by Bouchet et al. (2017) it contains eight families: Charopidae Hutton, 1884 (Australia, New Zealand, New Caledonia, Malesia, Oceania, Central and South America, St Helena, Southern Africa), Cystopeltidae Cockerell, 1891 (Australia), Discidae Thiele, 1931 (Holarctic), Endodontidae Pilsbry, 1895 (Oceania), Helicodiscidae Pilsbry, 1927 (North and Central America, Malesia, Australia), Oopeltidae Cockerell, 1891 (Southern Africa), Oreohelicidae Pilsbry, 1939 (North America), and Punctidae Morse, 1864 (nearly cosmopolitan, except for Central and South America).

The classification of the group has been historically unstable. Firstly, its family-level composition has differed markedly from author to author (e.g., Solem 1983; Nordsieck 1986, 2014; Tillier 1989; Schileyko 2001, 2002, 2006, 2007; Bouchet and Rocroi 2005; Bouchet et al. 2017). Secondly, many of the family-level taxa that have been proposed have subsequently been treated as synonyms. For instance, Bouchet et al. (2017) listed three synonyms of Punctidae and ten of Charopidae. Those authors erred in reassigning Oopeltidae to Punctoidea, with anatomical and molecular phylogenetic studies (Sirgel

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2012; Teasdale 2017) indicating that this family is more closely related to Arionoidea Gray, 1840.

Representatives of families Charopidae, Punctidae and Discidae were included in ribosomal RNA phylogenetic analyses by Wade et al. (2001, 2006). Those authors' trees showed, albeit with weak support, that Discidae are not closely related to Punctidae and Charopidae. The systematic relationships of Punctidae and Charopidae were not resolved in those analyses, as noted by Bouchet et al. (2017). In those works, *Laoma* Gray, 1850 (Punctidae) and *Suteria* Pilsbry, 1892 (Charopidae) formed a poorly-supported clade, with *Otoconcha* Hutton, 1883 (Charopidae: Otoconchinae Cockerell, 1893) as a sister group, thus rendering Charopidae paraphyletic. Bouchet et al. (2017: 386) noted that "if confirmed, it would indicate that the Charopidae in the broadly defined sense of Solem (1983) would have to be divided into separate families". A phylogenetic study of Panpulmonata by Teasdale (2017), using transcriptome and exon capture, included two species of Charopidae, from Australia and South Africa respectively, and one species each of Cystopeltidae and Punctidae. This analysis recovered a strongly-supported monophyletic Punctoidea, closely related to Oopeltidae, Caryodidae Connolly, 1915 and Rhytidoidea Pilsbry, 1893. Within Punctoidea the charopid taxa *Mulathena* Smith & Kershaw, 1985 and *Trachycystis* Pilsbry, 1893 grouped together, and *Cystopelta* and the punctid taxon *Paralaoma* Iredale, 1913 formed a separate, well-supported group.

The present study is a first attempt at determining a global phylogeny of the Punctoidea, incorporating taxa from all the constituent families listed by Bouchet et al. (2017), except Oopeltidae, and using a combination of mitochondrial and nuclear markers to infer a phylogeny for this superfamily.

Material and methods

Over 50 museums and universities worldwide were contacted in search of specimens, but only seven of those were able to provide preserved material that was suitable for molecular analysis (a few institutions had suitable specimens but declined to loan them). We tried to obtain representatives of as many genera, subfamilies and families of putative Punctoidea as possible, with preference given to type species of genera (and type genera of family/subfamily), and specimens from or near type localities.

The difficulty of obtaining specimens suitable for molecular analysis was not entirely unexpected. From our experience, tissues of punctoid snails, especially minute ones, are commonly in poor condition in museum collections. There are two main reasons for this: (1) snails sorted from soil/leaf litter samples can be dead and partly decomposed prior to preservation. (2) Live specimens that are killed by being put directly into ethanol retract into their shell, sometimes with copious production of mucus, and this can prevent ethanol penetrating all tissues (some decomposition then occurs in those tissues).

Overall, we obtained specimens of 50 species from seven of the eight punctoid families recognized by Bouchet et al. (2017) (Table 1). We did not include any representatives of Oopeltidae, which is more closely related to Arionoidea (see above). Our analysis included putative punctoid species assigned to families Charopidae (27 species), Cystopeltidae (1 species), Discidae (15 species), Endodontidae (1 species), Helicodiscidae (2 species), Oreohelicidae (4 species) and Punctidae (6 species). It included taxa from South Africa (1 species), Australia (4 species), New Zealand (17 species), Oceania (2 species), Central and South America (7 species), North America (23 species) and Europe (4 species). For three species, we included two specimens each from different geographic regions (i.e., USA vs Canada, NE vs SE Brazil). Data for three additional punctoid species were gathered from NCBI GenBank (Table 1); we used only sequence data stemming from published works with reliable identifications, voucher specimens, locality data, and sequence data for our markers of interest. All the specimens sequenced herein had their identification determined by comparison with type material or illustrations of type material where feasible, or from taxonomic literature and reference material in museum collections (details listed in Suppl. material 1: Part I).

We used as outgroups two species of Hygrophila, one of Succineidae, and one of Rhytididae, rooting the phylogeny using Hygrophila; Rhytididae was used to test the monophyly of Punctoidea in the first instance (see below). Sequence data of these species were taken from GenBank (Table 1), with the exception of the succineid, which was sequenced by us.

The specimens that we analyzed had either a small section of the foot clipped or (in the case of extremely minute specimens) were completely used for DNA extraction (standard protocol, QIAGEN DNEasy Blood & Tissue Kit; or 5% Chelex 100 solution, see Spencer et al., 2006). Roughly one third of our extractions failed due to poor specimen preservation, as explained above. We targeted four markers: (1) the barcoding fragment of the mitochondrial COI gene (primers LCO and HCO; Folmer et al., 1994), with circa 650 bp; (2) the mitochondrial 16S rRNA gene (primers 16SarL and 16SbrH; Simon et al., 1994), with circa 450 bp; (3) and (4) a continuous fragment of nuclear DNA encompassing the 3′ end of the 5.8S rRNA gene, the ITS2 region, and the 5′ end of the 28S rRNA gene, with a total of around 1,300 bp, that was amplified in two fragments. The primers used were LSU-1 and LSU-3 for the first fragment and LSU-2 and LSU-5 for the second fragment (Wade and Mordan 2000; Wade et al. 2006).

PCR amplification for COI and 16S involved an initial denaturation at 96 °C (2 min); followed by 35 cycles of denaturation at 94 °C (30 s), annealing at 48 °C (1 min) and extension at 72 °C (2 min); finishing with a final extension at 72 °C (5 min). The PCR protocol for ITS2+28S was performed with an initial denaturation at 95 °C (3 min); then 40 cycles of denaturation at 95 °C (30 s), annealing at either 50 °C (ITS2 section) or 45 °C

(28S section) (1 min) and (4) extension at 72 °C (2 min); followed by a final extension at 72 °C (4 min). Small variations of these protocols (e.g., annealing temperature, length of cycle steps) were used for some samples that initially failed to amplify.

PCR products were quantified via agarose gel electrophoresis, cleaned with ExoSAP-IT™ (Affymetrix Inc.), and Sanger sequenced. Sequences were assembled in Geneious Prime (v. 2019.0.3, Biomatters Ltd.), quality-checked, and uploaded to GenBank (Table 1). Alignment of sequences was also done in Geneious Prime with the MUSCLE plugin (Edgar 2004) using default settings (i.e., optimized for accuracy). The resulting alignment of each marker was manually proofed for errors and then run through Gblocks (Talavera and Castresana 2007), with the least restrictive settings available, in order to eliminate poorly aligned and divergent positions that might interfere with the analyses.

The sequences of each marker (COI, 16S, and ITS+28S) were then concatenated for a single phylogenetic analysis. Before concatenation, however, each marker was analyzed separately to search for conflicts between the resulting trees; no meaningful conflict was found. Phylogenetic analyses were performed with MrBayes 3.2.6 (Ronquist et al., 2012) for Bayesian Inference (henceforth BI) and the PhyML 3.0 online portal (Guindon et al. 2010) with maximum likelihood (henceforth ML).

For BI two concurrent analyses were run, each with four Markov chains of 20 million generations with the first 20% of samples discarded as 'burn-in', the default priors, nst = 6, rates = invgamma, temperature parameter = 0.1, sampling every 1,000 generations and the substitution model parameters unlinked across the three loci. MCMC convergence was assessed by examining the standard deviation of split frequencies and effective sample sizes (ESS) values in Mr Bayes and examining likelihood plots in Tracer v.1.7.1 (Rambaut et al. 2018). For ML, we used smart model selection (Lefort et al. 2017) with Akaike Information Criterion (AIC), subtree pruning-regrafting branch swapping and 2,000 bootstrap replicates.

A subset of our Punctoidea ingroup (17 species) was used alongside 23 other stylommatophoran snails (and 2 Hygrophila as outgroup) to further investigate the polyphyletism of Punctoidea and the position of its component branches within the whole group. The methodology is similar to the above and is discussed in detail in the Suppl. material 1: Part II, including a list of all species and their GenBank accession numbers (Suppl. material 1: Table S1).

Results

Taxonomic coverage

Our analysis was based on sequence data from taxa in seven of the eight families that Bouchet et al. (2017) assigned to Punctoidea, but coverage was not equal for all families (Table 1). Charopidae, Discidae, Oreohelicidae and Punctidae were each represented by multiple samples. Just under half the sampled species belong to Charopidae, with three of the presently recognized subfamilies being represented, namely Charopinae, Otoconchinae and Rotadiscinae Baker, 1927. Cystopeltidae and Endodontidae were represented by just one species each. Helicodiscidae was represented by GenBank data only (DNA extraction from additional helicodiscid specimens that we procured was unsuccessful). In any event we achieved relatively broad coverage for our ingroup, which included 53 species and 56 terminal branches (as there are three species each represented by two individuals).

Sequence data

After selection through Gblocks, our resulting concatenated alignment was 2196 bp long, with 1176 variable characters of which 935 were parsimony informative. Gblocks maintained 683 bp in the COI fragment, 387 bp in the 16S, and 1126 bp in the IT2+28S. We were unable to obtain high-quality 16S sequence data for four species (Table 1).

Phylogenetic analyses

The BI and the ML analyses returned nearly identical trees, so we present here the Bayesian phylogeny only (Fig. 1, but also including the ML support values). The ML tree had some minor differences regarding the placement of the charopid taxa *Allodiscus* Pilsbry, 1892, *Chalcocystis* Watson, 1934, *Otoconcha*, and Chilean *Radiodiscus* sp., but all with very little support. For clarity, we refer below only to BI posterior probability (PP) values, while the ML support values can be seen in Fig. 1.

The resulting tree shows that Punctoidea is not monophyletic (Fig. 1), a possibility that had already been alluded to by some previous authors (e.g., Wade et al. 2001, 2006; Holyoak et al. 2011; Nordsieck 2014). Rather, it is widely polyphyletic (see also the more comprehensive polyphyletism test in the Suppl. material 1: Part II), consisting of three distinct and well-supported groups within suborder Helicina: (1) a group containing Discidae and Oreohelicidae (1.0 PP), which we refer to a new superfamily Discoidea, based on the earliest available family-group name; (2) the Helicodiscidae, which forms a separate strongly supported group (1.0 PP) of uncertain affinity within suborder Helicina, in Stylommatophora; and (3) the Punctoidea sensu stricto, containing Endodontidae, Cystopeltidae, Punctidae and paraphyletic Charopidae (1.0 PP). Because the fossil record of Punctoidea sensu stricto is poorly understood (see Discussion below), and some of the internal branches of our phylogeny were not strongly supported, we have not attempted to estimate divergence times based on the molecular data.

Table 1. List of species used in the present work, with their respective GenBank registration number for each marker, voucher specimen information, and collection locality. Families are listed according to former classification, that is, before the present work; species which were allocated in different families after our analysis are marked with an asterisk (see also Fig. 1). Sequence data extracted from GenBank is identified as so in the 'Voucher' column. Taxa noted as 'sp.' represent juvenile specimens that could only be identified to genus level. Institution acronyms: FMNH = Field Museum of Natural History (Chicago, USA), MZSP = Museu de Zoologia da Universidade de São Paulo (São Paulo, Brazil); NMNZ = Museum of New Zealand Te Papa Tongarewa (Wellington, New Zealand); NMW = National Museum Wales (Cardiff, UK); OZD = University of Otago (Dunedin, New Zealand); RBCM = Royal British Columbia Museum (Victoria, Canada); TMAG = Tasmanian Museum and Art Gallery (Hobart, Australia).

Species	COI	16S	ITS2+28S	Voucher	Locality
ACROLOXIDAE					
Acroloxus lacustris (Linnaeus, 1758)	AY282581	–	–	GenBank	Germany, Brandenburg, Harnekop, Großer See
Acroloxus lacustris (Linnaeus, 1758)	–	EF489311	EF489364	GenBank	Germany
CHAROPIDAE					
Allodiscus dimorphus (Reeve, 1852)	MN792581	MN756708	MN782439	OZD Adimo-5	New Zealand, Auckland, Waitakere Ranges, Titirangi, Atkinson Track
Alsolemia longstaffae (Suter, 1913)	MN792582	MN756709	MN759313	OZD Almon-1	New Zealand, Southland, Colac Bay
Chalcocystis aenea (F. Krauss, 1848)	MN792590	MN756717	MN782447	NWM.Z.2001.004.00939	South Africa, KwaZulu-Natal, Hluhluwe
Charopa coma (Gray, 1843)	MN792591	MN756718	MN782448	OZD Chcom-5	New Zealand, Auckland, Waitakere Ranges, Titirangi, Paturoa Stream
Diemenoropa kingstonensis (Legrand, 1871)*	MN792616	MN756740	MN782473	TMAC E26620	Australia, Tasmania, Skullbone Plains, Kenneth Lagoon
Fectola infecta (Reeve, 1852)	MN792600	MN756727	MN782457	OZD Feinf-1	New Zealand, Waikato, Coromandel Peninsula, Port Charles
Flammulina zebra (Le Guillou, 1842)	MN792601	MN756728	MN782458	OZD Flzeb-1	New Zealand, Tasman, Lake Daniells
Lilloiconcha gordurasensis (Thiele, 1927)*	MN792604	MN756731	MN782461	MZSP 133646	Brazil, Alagoas, Pedra Talhada Biological Reserve
Lilloiconcha gordurasensis (Thiele, 1927)*	MN792605	–	MN782462	MZSP 106118	Brazil, São Paulo, São Paulo, Burle Marx Park
Lilloiconcha superba (Thiele, 1927)*	MN792606	–	MN782463	MZSP 133637	Brazil, Alagoas, Pedra Talhada Biological Reserve
Mitodon wairarapa (Suter, 1890)	MN792607	MN756732	MN782464	OZD Miwai-1	New Zealand, Southland, Stewart Island, Mason Bay, Gutter
Mocella eta (Pfeiffer, 1853)	MN792608	MN756733	MN782465	OZD Moeta-1	New Zealand, Northland, Umuheke Bay
Neophenacohelix giveni (Cumber, 1961)	MN792609	MN756743	MN782466	OZD Phgiv-1	New Zealand, Northland, Whangarei, Coronation Reserve
Otoconcha dimidiata (L. Pfeiffer, 1853)	MN792614	MN756738	MN782471	OZD Otdim-1	New Zealand, Northland, Whangarei, Bream Head
Phacussa helmsi (Hutton, 1882)	MN792618	MN756742	MN782475	OZD Phhel-2	New Zealand, West Coast, Greymouth, Point Elizabeth
Phenacohelix pilula (Reeve, 1852)	MN792619	MN756744	MN782476	OZD Phpil-1	New Zealand, Northland, Whangaruru North Head
Radioconus amoenus (Thiele, 1927)	MN792623	MN756749	MN782481	MZSP 135899	Brazil, Santa Catarina, Florianópolis, Gruta do Triângulo
Radiodomus abietum (H.B. Baker, 1930)*	MN792624	MN756750	MN782482	FMNH 386227	USA, Idaho, Seven Devils Mountains, Seven Devils Road
Radiodiscus sp.	MN792625	MN756751	MN782483	MZSP 100219	Brazil, Bahia, Ilhéus
Radiodiscus sp.	MN792626	MN756752	MN782484	FMNH 331252	Chile, Chiloé, Chiloé National Park, Chepu
Ranfurlya constanceae Suter, 1903	MN792627	MN756753	MN782485	OZD Racon-1	New Zealand, Auckland Islands, Adams Island
Scelidoropa officeri (Legrand, 1871)*	MN792617	MN756741	MN782474	TMAC E28374	Australia, Tasmania, Flinders Island, Brougham Sugarloaf
Sinployea atiensis (Pease, 1870)	MN792628	MN756754	MN782486	NMNZ M.283340	Cook Islands, Rarotonga, Tupapa Valley
Stenacapha hamiltoni (Cox, 1868)	MN792629	MN756755	MN782487	TMAC E28243	Australia, Tasmania, Central Plateau, Viormy
Suteria ide (Gray, 1850)	MN792630	MN756756	MN782488	OZD Suide-3	New Zealand, Manawatu-Wanganui, Bushy Park
Therasia thaisa Hutton, 1883	MN792631	MN756757	MN782489	OZD Ththa-6	New Zealand, Southland, Clifden, Clifden Limestone Cave System
Zilchogyra sp.*	MN792632	–	MN782490	MZSP 102889	Brazil, São Paulo, Cotia, Morro Grande Reserve
CYSTOPELTIDAE					
Cystopelta bicolor Petterd & Hedley, 1909	MN792592	MN756719	MN782449	TMAC E26659	Australia, Tasmania, Bronte Park
DISCIDAE					
Anguispira alternata (Say, 1816)	MN792583	MN756710	MN782440	NMNZ M.326602	Canada, Ontario
Anguispira alternata (Say, 1816)	MN792584	MN756711	MN782441	FMNH 380947.2	USA, Illinois, Sangamon

Species	COI	16S	ITS2+28S	Voucher	Locality
Anguispira jessica Kutchka, 1938	MN792585	MN756712	MN782442	FMNH 383610	USA, North Carolina, Macon
Anguispira kochi (L. Pfeiffer, 1846)	MN792586	MN756713	MN782443	RBCM 015-00446-001	Canada, British Columbia, Bear Creek
Anguispira kochi (L. Pfeiffer, 1846)	MN792587	MN756714	MN782444	FMNH 372699	USA, Illinois, Brown
Anguispira nimapuna H.B. Baker, 1932	MN792588	MN756715	MN782445	FMNH 386201	USA, Idaho, Lowell, Rye Patch Creek
Anguispira strongyloides (Pfeiffer, 1854)	MN792589	–	–	FMNH 384431	USA, Alabama, Stevenson, County Rd. 172
Anguispira strongyloides (Pfeiffer, 1854)	–	MN756716	MN782446	NMNZ M.326603	USA, Florida
Discus catskillensis (Pilsbry, 1896)	MN792593	MN756720	–	NMNZ M.328403	Canada, New Brunswick, Spednic Lake Protected Natural Area
Discus catskillensis (Pilsbry, 1896)	–	–	MN782450	NMNZ M.328404	Canada, New Brunswick, Spednic Lake Provincial Park
Discus nigrimontanus (Pilsbry, 1924)	MN792594	MN756721	MN782451	FMNH 383556	USA, Alabama, Jackson
Discus patulus (Deshayes, 1830)	MN792595	MN756722	MN782452	FMNH 383604	USA, North Carolina, Macon
Discus perspectivus (Megerle von Mühlfeld, 1816)	MN792596	MN756723	MN782453	NMNZ M.326601	Czech Republic, Olomouc, **Střeň**, Litovelské Luhy Nature Reserve
Discus rotundatus (O.F. Müller, 1774)	FJ917285	FJ917265	FJ917212	GenBank	Germany, Hesse, Frankfurt am Main
Discus ruderatus (Hartmann, 1821)	MN792597	MN756724	MN782454	FMNH 316093	Italy, Trentino-Alto Adige
Discus shimeki (Pilsbry, 1890)	MN792598	MN756725	MN782455	RBCM 004-00130-001	Canada, British Columbia, Liard Plain
Discus whitneyi (Newcomb, 1864)	–	–	MN782456	RBCM 016-00152-003	Canada, British Columbia, Elmer Creek
Discus whitneyi (Newcomb, 1864)	MN792599	MN756726	–	RBCM 016-00163-002	Canada, British Columbia, Teepee Creek
ENDODONTIDAE					
Libera fratercula (Pease, 1867)	MN792603	MN756730	MN782460	NMNZ M.282580	Cook Islands, Rarotonga, Tupapa
HELICODISCIDAE					
Helicodiscus barri Hubricht, 1962	MK675003	MK541116	–	GenBank	USA, Tennessee, Vanleer, Columbia Cave
Helicodiscus parallelus (Say, 1821)	KT707362	–	–	GenBank	Canada, Ontario, Cambridge, Charitable Research Reserve
Helicodiscus parallelus (Say, 1821)	–	–	DQ256731	GenBank	USA?
OREOHELICIDAE					
Oreohelix idahoensis (Hemphill, 1890)	MN792610	MN756734	MN782467	FMNH 386247	USA, Idaho, Lucile, Salmon River
Oreohelix strigosa depressa Pilsbry, 1904	MN792611	MN756735	MN782468	FMNH 374603	USA, Colorado, Garfield
Oreohelix subrudis (Reeve, 1854)	MN792612	MN756736	MN782469	RBCM 012-00297-001	Canada, British Columbia, Flathead Service Road
Oreohelix vortex S.S. Berry, 1932	MN792613	MN756737	MN782470	FMNH 386172	USA, Idaho, White Bird, Old Highway 95
PLANORBIDAE					
Planorbis planorbis (Linnaeus, 1758)	EF012175	–	–	GenBank	Germany, Brandenburg, Obersdorf, Vordersee
Planorbis planorbis (Linnaeus, 1758)	–	EF489315	EF489369	GenBank	Germany
PUNCTIDAE					
Laoma leimonias (Gray, 1850)	MN792602	MN756729	MN782459	OZD Lalem-1	New Zealand, Northland, Kaihu, Maropiu Road
Paralaoma servilis (Shuttleworth, 1852)	MN792615	MN756739	MN782472	OZD Paser-2	New Zealand, Southland, Colac Bay
Phrixgnathus celia Hutton, 1883	MN792620	MN756745	MN782477	OZD Phcel-1	New Zealand, Southland, Stewart Island, Mason Bay
Punctum californicum Pilsbry, 1898	MN792621	MN756746	MN782478	NMNZ M.328402	USA, California, San Francisco, Presidio, Lincoln Boulevard
Punctum pygmaeum (Draparnaud, 1801)	MN812719	MN756747	MN782479	NMW.Z.2017.008.00537	UK, Monmouthshire, Monmouth, Pentwyn Farm
Punctum randolphii (Dall, 1895)	MN792622	MN756748	MN782480	NMNZ M.328401	Canada, British Columbia, Pemberton, Riverside Trail, Lillooet River
RHYTIDIDAE					
Rhytida greenwoodi (Gray, 1850)	KT970868	KT970900	KP230525	GenBank	New Zealand, Waikato, Raglan
SUCCINEIDAE					
Succinea manaosensis Pilsbry, 1926	MN186467	MN186468	MN186473	NMNZ M.325472	Brazil, Paraíba, Areia, Centro de Ciências Agrárias

Discussion

Systematics: Discoidea

This superfamily is strongly supported (Fig. 1) and is overall very well resolved, with all internal branches equally well supported. It contains two distinct groups, the families Oreohelicidae and Discidae. Our analysis of wider relationships within Stylommatophora (see Suppl. material 1: Part II) placed Discoidea close to infraorder Helicoidei, with strong support in the BI tree but weak support in the ML tree.

Oreohelicidae: This family, which is endemic to North America, is a strongly supported (1.0 PP) monophyletic group that is separate from Discidae and basal within Discoidea.

Discidae: This is a well-supported (1.0 PP) monophyletic group, which includes *Anguispira* Morse, 1864 and *Discus* Fitzinger, 1833. Our analysis indicates that the former genus is monophyletic, but the latter, as currently interpreted, is paraphyletic. This is not unexpected as *Discus* has been used a wastebasket taxon for North American and European discoid species, both Recent and fossil. However, what was surprising is that whereas two European species of *Discus* formed a separate basal clade (1.0 PP), a third European species, which was identified as *D. ruderatus* (Hartmann, 1821), the type species of the genus, grouped with North American species (1.0 PP). Further work is required to resolve the genus-level taxonomy of the species presently assigned to *Discus*, as well as the phylogenetic relationships of putative discid taxa from the Canary Islands (Holyoak et al. 2011; Cameron et al. 2013).

Our analysis indicated that samples identified as *Anguispira alternata* (Say, 1817) from the USA and Canada were very similar genetically and probably conspecific with one another. In contrast, the samples identified as *A. kochi* (Pfeiffer, 1846) from the USA and Canada differed markedly from one another, indicating that this taxon, which has a complex synonymy (MolluscaBase 2020), and is currently recognized as having a strongly disjunct distribution in North America, is probably a species complex.

Discoidea *incertae sedis*: The monotypic North American genus *Radiodomus* H.B. Baker, 1930 has previously been classified in subfamily Rotadiscinae of Charopidae, although Pilsbry (1948b) noted that the type species, *Radiodomus abietum* Baker, 1930, differed anatomically from other rotadiscines. Our phylogenetic analysis indicates that *Radiodomus* belongs instead in Discoidea, but further work is required to determine if it should be treated as the basal taxon in Discidae, or assigned to a separate, new family-level group within Discoidea.

Systematics: Helicodiscidae

This family is native to Central and North America (Zilch 1959). A species of helicodiscid that has been described from southeastern Brazil (Simone 2006) is actually an adventive North American species (Silva et al. 2020). *Stenopylis coarctata* (Möllendorff, 1894), which is apparently native to Malesia and northern Australia, has also been assigned to Helicodiscidae (e.g., Solem 1984; Stanisic et al. 2010), but this family-level classification requires reevaluation.

In our phylogeny Helicodiscidae is represented by two North American species of *Helicodiscus* Morse, 1864 that form a strongly supported (1.0 PP) clade. Although previously included in Punctoidea, our analysis suggests that Helicodiscidae does not belong in either Discoidea or the redefined Punctoidea. Its phylogenetic relationships with other taxa have not been precisely determined (see Suppl. material 1), but both our ML and BI trees position it (albeit with low support) close to Arionoidea and the 'limacoid clade' (now infraorder Limacoidei; Bouchet et al., 2017). As such the family is treated here as *incertae sedis* within suborder Helicina (in Stylommatophora), pending further work. Oopeltidae has also been previously classified in Punctoidea (Bouchet et al. 2017), although shown to be more closely related to Arionoidea (Sirgel 2012); whether or not Oopeltidae is closely related to Helicodiscidae requires investigation.

Systematics: Punctoidea

The Punctoidea, as redefined here, is a strongly supported clade (1.0 PP) clade containing representatives of Endodontidae, Cystopeltidae, Punctidae and Charopidae (Fig. 1). We could not reliably determine its position within Stylommatophora: our ML tree placed it as the basal group within suborder Helicina, while our BI placed it in a more derived position within Helicina (see Suppl. material 1: Part II).

Endodontidae: In our analysis, this family is represented by one species only, in the Polynesian genus *Libera* Garrett, 1881, but its split from the other punctoids is clear and strongly supported (1.0 PP). As such, Endodontidae is basal in the redefined Punctoidea, and is the sister taxon of the clade formed by the other punctoid families, as redefined below.

Cystopeltidae: Previously this family was interpreted as containing a single genus of semi-slugs, *Cystopelta* Tate, 1881, endemic to southeastern Australia, but our analysis indicated strong support (1.0 PP) for a monophyletic family-level group comprising two strongly supported clades (both 1.0 PP): one containing *Cystopelta bicolor* Petterd & Hedley, 1909, and two Tasmanian land snail taxa that were previously assigned to Charopidae, *Diemenoropa kingstonensis* (Legrand, 1871) and *Scelidoropa officeri* (Legrand, 1871); and the other containing South American land snail species in the genera *Lilloiconcha* Weyrauch, 1965 and *Zilchogyra* Weyrauch, 1965, which were previously assigned to Charopidae as well. These two clades possibly warrant separate subfamily-group status, but further work is required to test this. Our results indicate that the genus- and species-level

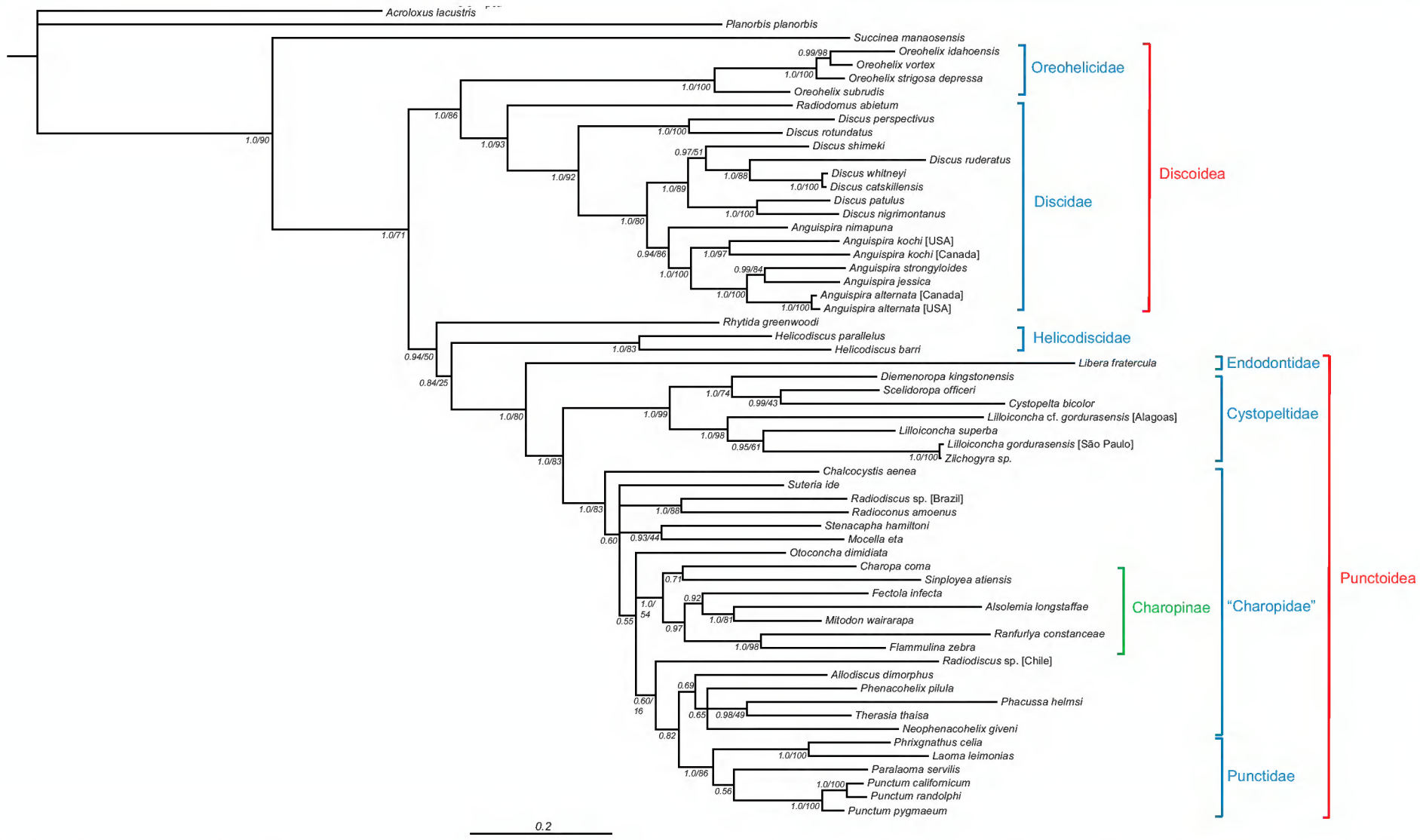

Figure 1. Bayesian tree for the "Punctoidea", rooted by the Hygrophila. Numbers shown on nodes are BI posterior probabilities (0 to 1) followed by ML bootstrap values (0 to 100%). Scale bar is substitutions per site.

classification of *Lilloiconcha* and *Zilchogyra* is in need of revision, as already alluded to by previous authors (e.g., Salvador et al. 2018b; Salvador 2019).

The charopid taxa that grouped in Cystopeltidae in our analysis have very similar shell morphology to some charopid taxa in the Punctidae + Charopidae clade (below). For the South American cystopeltid branch at least, a smooth protoconch might be a diagnostic character (Schileyko 2001). However, for many charopid genus groups it may not be possible to assign taxa to either family on the basis of shell characters alone. Further work is required to determine the family-level placement of the numerous extant taxa that are currently assigned to Charopidae but which were not included in our analysis, as well as to determine reliable family-level diagnostic characters.

The phylogenetic relationships of Cystopeltidae in our analysis appear to differ from the findings of Teasdale (2017), which indicated that *Cystopelta purpurea* Davies, 1912 (Cystopeltidae), and a putative representative of Punctidae that was identified as *Paralaoma* sp. (misspelled as *Paraloama* in the original), were sister species, separate from a group of two charopid species from Australia and South Africa, respectively. The reasons for this difference are unclear. It may be an artefact of the small number of punctoid samples and restricted geographic range in Teasdale's (2017) analysis compared with our study.

Punctidae + Charopidae clade: Our analysis indicates strong support (1.0 PP) for a clade incorporating taxa that were previously assigned to Punctidae and Charopidae (excluding those that grouped with Cystopeltidae, see above). The phylogenetic relationships determined here suggest that whereas Punctidae, as previously interpreted, is monophyletic, Charopidae sensu Solem (1983: 47) and later authors is paraphyletic. At present there is insufficient information to determine whether Charopidae Hutton, 1884 would be best treated as a junior synonym of Punctidae Morse, 1864, or split into a series of separate monophyletic family units. In the meantime, for taxonomic stability, we suggest that Charopidae should be retained as a separate, paraphyletic family-level group, pending further work to determine the phylogenetic relationships of its constituent taxa (below).

The family-group name Punctidae is used here for a well-supported clade (1.0 PP), within which there is a strongly supported (1.0 PP) basal group containing the endemic New Zealand taxa *Laoma* Gray, 1850 and *Phrixgnathus* Hutton, 1882, corresponding to Laominae Suter, 1913, and a weakly supported group (0.56 PP) containing *Paralaoma*, which is native to Australasia but has a wide adventive distribution, and type genus *Punctum* Morse, 1864. As presently interpreted the latter genus has a predominantly Holarctic distribution in North America, Japan and extratropical Eurasia, but with records also from Central America, Hawai'i and tropical Africa (Pilsbry 1948b; Cowie et al. 1995; Wronski and Hausdorf 2010; de Winter 2017; Horsák and Meng 2018). Punctidae probably also includes other New Zealand punctid taxa

listed by Spencer et al. (2009) and Australian punctid taxa listed by previous authors (e.g., Smith 1992; Schileyko 2002; Stanisic et al. 2010, 2018).

The family-group name Charopidae is provisionally retained here for charopid taxa other than those reassigned to Cystopeltidae (above). It includes taxa previously assigned to Charopinae Hutton, 1884 (in part), Phenacohelicidae Suter, 1892, Otoconchinae Cockerell, 1893, Flammulinidae Crosse, 1895, Patulastridae Steenburg, 1925, Rotadiscinae, Trachycystidae Schileyko, 1986, Ranfurlyinae Schileyko, 2001, and Therasiinae Schileyko, 2001. This diverse group of taxa has a very wide distribution that includes South America, South Africa, Australia, New Zealand and Oceania. The relationships within this group are as yet poorly resolved (see below), but our analysis indicates that it contains at least one strongly-supported group (1.0 PP), corresponding to Charopinae sensu stricto, which includes the type genus *Charopa* Albers & Martens, 1860, some other New Zealand taxa, and *Sinployea* Solem, 1983 from Oceania. Two of the constituent taxa, *Flammulina* E. von Martens, 1873 and *Ranfurlya* Suter, 1903, are the type genera of Flammulinidae and Ranfurlyinae, respectively, confirming that the latter two taxa are synonyms of Charopinae. Conversely, our analysis indicates that Charopinae does not include some genus-groups such *Mocella* Iredale, 1915, *Stenacapha* Smith & Kershaw, 1985 and *Suteria* Pilsbry, 1892, that were assigned to it by previous workers (e.g., Schileyko 2001).

Many of the charopid taxa in our analysis could not be reliably assigned to subfamily groups. The basal-most charopid taxon in our phylogeny is the African genus *Chalcocystis* Watson, 1934. It has been referred to the subfamily Trachycystinae (e.g., Schileyko 2001), but other authors have treated this subfamily as a synonym of Charopinae (e.g., Bouchet et al. 2017). This branch is strongly separated from the remaining punctoids, which suggests that Trachycystinae may have some biological reality if restricted to African taxa. Analysis of a larger sample of African taxa, including the type genus of the subfamily, is required to reliably determine the systematic relationships of this group.

The genus of semi-slugs *Otoconcha* forms a separate lineage in our analysis, albeit with poor support (0.55 PP). *Otoconcha* and *Maoriconcha* Dell, 1952 have been assigned to the endemic New Zealand subfamily Otoconchinae (e.g., Schileyko 2001), but further work is required to determine the phylogenetic relationships of these genera and the taxonomic status of Otoconchinae.

The New Zealand charopid taxon *Suteria* Pilsbry, 1892 also forms a separate lineage with poor support (0.6 PP) in our analysis. It was previously included in Charopinae (e.g., Schileyko 2001). Four other New Zealand "charopid" taxa, *Neophenacohelix* Cumber, 1961, *Phenacohelix* Suter, 1892, *Phacussa* Hutton, 1883 and *Therasia* Hutton, 1883, formed a poorly supported group (0.65 PP). The two first-named and two last-named taxa were previously assigned to Phenacohelicinae and Therasiinae, respectively. In our Bayesian tree, the New Zealand taxon *Allodiscus* Pilsbry, 1892, previously assigned to Phenacohelicinae (*e.g.*, Schileyko 2001), grouped with these four taxa albeit with poor support (0.69 PP); in the ML tree, however, it was the sister taxon to Punctidae, again with poor support (50).

Stenacapha Smith & Kershaw, 1985 from Australia and *Mocella* Iredale, 1915 from New Zealand, both formerly included in Charopinae, formed a separate group in our analysis, albeit with moderate support only (0.93 PP).

Three of the South American taxa that were included in our analysis belong in two separate groups within the Punctidae + Charopidae clade. *Radioconus amoenus* (Thiele, 1927) and the Brazilian *Radiodiscus* sp. form a strongly supported group (1.0 PP), but the Chilean *Radiodiscus* sp. belongs to a separate lineage. *Radiodiscus*, as previously interpreted, is evidently polyphyletic; this is not unexpected, as the genus has historically functioned as a wastebasket taxon for South American charopids. Whether one or both these groups should have subfamily status, and whether or not either of them corresponds to Rotadiscinae, has not been determined. In any event, it is clear that New Zealand taxa that were assigned to Rotadiscinae by Climo (1989) and subsequent workers, including the genera *Alsolemia* Climo, 1981 and *Mitodon* Climo, 1989, belong instead in Charopinae (Fig. 1).

Several family-level taxa that have previously been treated as synonyms of Charopidae, or subfamily-groups within Charopidae, were not included in the analysis. These include (in chronological order): Amphidoxinae Thiele, 1931 (Chile); Dipnelicidae Iredale, 1937 (Australia); Hedleyoconchidae Iredale, 1942 (Australia); Pseudocharopidae Iredale, 1944 (Lord Howe Island); Semperdoninae Solem, 1976 (Micronesia); Trukcharopinae Solem, 1983 (Micronesia); and Flammoconchinae Schileyko, 2001 (New Zealand). Thysanotinae Godwin-Austen, 1907 (southern Asia and Pacific islands) has been included in Charopidae by some authors (e.g., Bouchet et al., 2017), but ongoing studies suggest that it does not belong in Punctoidea (Fred Naggs, pers. comm.).

The poor resolution in our analysis of some phylogenetic relationships within Charopidae may have been because of insufficient sequence information or inadequate sampling of taxa. The latter is more likely, given that the sequence data were sufficient to resolve phyletic relationships with strong support within the other families that were examined. Although the analysis included samples of 24 genus-level charopid taxa (Table 1), this represents only a very small proportion of the overall diversity of this paraphyletic group. For instance, the Australian fauna includes 104 named genus groups of charopids (Stanisic et al. 2010, 2018), of which we sampled three taxa (c 3%) only. In the New Zealand fauna, there are 45 named charopid genera (Spencer et al. 2009), 14 of which (31%) were included in our analysis. The fauna of Oceania includes 20 named charopid genera (Solem 1983), of which we sampled one taxon (5%) only. For large, diverse and reasonably old groups, it is deemed that adding taxa usu-

ally outweighs adding sequence data (Pollock et al. 2002; Zwickl and Hillis 2002; Heath et al. 2008; Nabhan and Sarkar 2011). Obtaining a better resolution of the subfamily-level groups within the clade of Punctidae + Charopidae will require a broader coverage of species, both taxonomically and geographically.

Paleobiogeography: Discoidea

This superfamily has a Laurasian distribution. Based on our present phylogeny of extant species, Oreohelicidae and *Radiodomus* are North American, and the most basal Discidae are European, while a group of more derived discids includes both European and North American taxa. The phylogenetic relationships of purported Discidae from the Canary Islands are as yet undetermined.

Records of land snails from the Carboniferous of North America that were attributed to Discidae and other stylommatophoran groups by Solem and Yochelson (1979) are now considered to be non-stylommatophoran eupulmonates (e.g., Bandel 1991, 1997; Mordan and Wade 2008). The oldest known fossil taxa assigned to Discoidea are from the Late Cretaceous of Alberta, Canada. They include *Discus sandersonae* (Russell, 1929), in family Discidae (Pilsbry, 1939), and *Oreohelix obtusata* (Whiteaves, 1885), *Radiocentrum anguliferum* (Whiteaves, 1885) and *R. thurstoni* (Russell, 1926), all in family Oreohelicidae, (Henderson 1935; Tozer 1956; Roth 1986). Other fossil species of *Radiocentrum* Pilsbry, 1905 are known from the Paleocene of Alberta, Eocene of Wyoming, and Oligocene of Colorado, whereas the Quaternary distribution of this genus group is restricted to southwestern USA and northwestern Mexico (Roth 1986; Hochberg et al. 1987). Fossil species of *Oreohelix* Pilsbry, 1904 are known from Late Cretaceous, Paleocene and Eocene faunas from Alberta to Utah (Roth 1986). *Oreohelix* is the most diverse genus group in the extant North American land snail fauna, with 79 species recorded from western Canada, USA and Mexico (Pilsbry 1948a, 1948b; Nekola 2014).

In North America relatively few fossil species of *Discus* sensu lato are known from the Cenozoic, with records from the Late Paleocene/Early Eocene of Utah, Eocene of Wyoming and Montana, and Miocene of Oregon (Pilsbry 1939; La Roque 1960; Pierce and Constenius 2014). In Europe the oldest known fossil taxon in Discidae is *Discus perelegans* (Deshayes, 1863) from the Late Paleocene/Early Eocene of the Paris Basin, France (Wenz 1923). *Discus* sensu lato evidently underwent an extensive radiation in the mid Paleogene of Europe, with several species represented in fossil faunas of Eocene age from southern England and the Paris Basin (Preece 1982; Pacaud and Le Renard 1995). The Neogene land snail fauna of Europe also contains numerous fossil species that have been assigned to this paraphyletic genus group (e.g., Harzhauser et al. 2014; Höltke et al. 2016, 2018).

Anguispira has a fossil and extant distribution restricted to North America. The oldest known fossil is *Anguispira* cf. *alternata* (Say, 1816) from the Eocene of Montana, USA (Pierce and Constenius 2014), indicating that the split between this genus and *Discus* sensu lato took place in the Eocene or earlier. The Discidae presumably diverged from the Oreohelicidae and *Radiodomus* lineages in the Late Cretaceous or earlier.

Paleobiogeography: Helicodiscidae

Fossils of helicodiscid taxa are known from the Early Miocene of Europe (genus *Lucilla* Lowe, 1852; Nordsieck 2014; Salvador 2014) and the Late Miocene of North America (Liggert 1997; Gladstone et al. 2019), indicating a former wider Laurasian distribution.

Paleobiogeography: Punctoidea

This superfamily is distributed almost worldwide, but given that the greatest diversity of extant taxa is in the Southern Hemisphere, with one genus only in the Northern Hemisphere, it is likely of Gondwanan origin. Interpretation of the biogeographic history of the Punctoidea is hindered by a relatively sparse fossil record, and the difficulty in reliably assigning fossil material, which in many cases is poorly preserved, to family-level groups on the basis of shell morphology alone. Our finding that some extant taxa that were previously assigned to Charopidae actually belong in Cystopeltidae has further complicated matters, because, as noted above, shell characters of charopid genus groups do not appear to be a reliable indicator of family-level phylogenetic relationships. Despite these limitations, some useful biogeographic information can be gleaned from the fossil record.

The oldest known fossil taxon that could possibly be assigned to Punctoidea is *Radiodiscus santacrucensis* Morton, 1999, from the Lower Cretaceous of Argentina (Morton 1999; Rodríguez et al. 2012), although the genus-level placement of this species is probably incorrect and requires re-evaluation (Salvador et al. 2018a), and the family-level placement is unclear. All other known fossils of Punctoidea are from the Cenozoic.

The oldest fossil species that can be reliably assigned to Endodontidae is *Cookeconcha subpacificus* (Ladd, 1958) from the Lower Miocene of Bikini Atoll, Marshall Islands (Ladd 1958). It is most closely related to Pleistocene and Recent congeners from Midway Atoll and Hawai'i, respectively (Solem 1976, 1977, 1983). The monotypic fossil taxon *Hebeispira hebeiensis* Youluo, 1978, of "Early Tertiary" age from the Bohai coastal plain in North China, was assigned to Endodontidae. However, examination of images of type material (Youluo 1978: pl. 30, figs 12–14) indicates that it belongs in neither Endodontidae nor Punctoidea and is likely a freshwater Planorbidae. Likewise, records of undetermined Endodontidae from the Early/Middle Miocene of Germany by Moser et al. (2009) have been refuted (Nordsieck 2014; Salvador and Rasser 2014).

The Endodontidae are otherwise known from Oceania only, on volcanic and uplifted islands between Tuvalu, Pitcairn Islands and Hawai'i, with an outlying genus-group in Palau, Micronesia (e.g., Solem 1976, 1983; Abdou and Bouchet 2000; Brook 2010; Sartori et al. 2014). No endodontids are known from the Holocene faunas of Marshall Islands and Midway Atoll. Taxa that were present there during mid to late Cenozoic time when these islands were high-standing presumably became extinct when the islands subsided and became atolls (Solem 1976). Similar histories of endodontid species colonizing oceanic islands by over-water dispersion, undergoing radiations at species and sometimes also genus level, and becoming extinct when host islands subsided to, and below, sea level, probably played out across much of Oceania during the Neogene and Quaternary, and probably also earlier in the Paleogene (see below).

Thirteen species of Cenozoic fossil land snails from South America have been included in Punctoidea with varying degrees of confidence (Miquel and Bellosi 2007; Rodriquez et al. 2012; Miquel and Rodríguez 2015; Salvador et al. 2018a). This includes species in extant genus groups that we have assigned to Cystopeltidae (i.e., *Lilloiconcha*, *Zilchogyra*) and the Punctidae + Charopidae clade (i.e., *Punctum*, *Radiodiscus*), along with other extant and extinct genus groups whose family-level placement has not been determined. The earliest fossil records of *Lilloiconcha*, *Radiodiscus* and *Zilchogyra* are from the Eocene of Argentina (Miquel and Bellosi 2007; Rodriquez et al. 2012), and the earliest (and only) record of *Punctum* from South America is from the Early/Middle Miocene of Argentina (Miquel and Rodríguez 2015; Salvador et al. 2018a). Even with uncertainties, this indicates that Cystopeltidae, Punctidae and 'Charopidae' existed in South America as separate lineages by Eocene time.

In New Zealand, where extant Punctoidea are extremely diverse at both genus and species level, the pre-Quaternary fossil record is unfortunately very limited. The oldest known fossils are seven species of Early Miocene age from Otago (Marshall and Worthy 2017). All but one of these species have been assigned to extant genera, with one in Punctidae (*i.e.*, *Paralaoma*), two in genera that our analysis indicated belong in Charopinae (i.e., *Charopa*, *Fectola* Iredale, 1915), and one other charopid genus (*Neophenacohelix*). The extinct genus *Atactolaoma* Marshall & Worthy, 2017 probably belongs in Punctidae, but the family and subfamily status of the charopid taxa *Cavellia* Iredale, 1915 and *Dendropa* Marshall & Worthy, 2017 has not been determined. As yet, we do not know if Cystopeltidae are and/or were ever present in the New Zealand region.

In Oceania, the only known pre-Quaternary fossil charopid is *Vatusila eniwetokensis* (Ladd, 1958) from the Late Miocene of Eniwetok Atoll, Marshall Islands (Solem 1976, 1983). This genus, which is genetically closely related to *Sinployea* (M. Kennedy, unpublished data) and probably belongs in Charopinae, has a Holocene distribution extending from Tuvalu south to Tonga and Niue (Solem, 1983). As with Endodontidae on Marshall Islands and Midway Atoll (see above), the distribution of *Vatusila* within Oceania evidently changed markedly during the Neogene, in response to patterns of over-water dispersion and the emergence and foundering of oceanic islands.

In Europe and North America, the Punctoidea is represented by one genus only, as noted above. The oldest putative fossil *Punctum* in Europe is *P. oligocaenicum* Zindorf, 1901 of Late Oligocene age from Germany (Wenz, 1923). However, Harzhauser et al. (2014) noted that this species may not belong to *Punctum*, and the family placement therefore also requires re-evaluation. Fossil species that undoubtedly belong in *Punctum* are well represented in Neogene strata in continental Europe (Harzhauser et al. 2014; Höltke et al. 2016). In North America the oldest putative fossil *Punctum*, and the only pre-Quaternary record of this genus, is *P. alveus* Pierce, 1992, from the Late Oligocene/ Early Miocene of Montana, USA (Pierce 1992).

Australia, like New Zealand, has a diverse extant punctoid fauna, but whereas the New Zealand fauna is dominated at the species level by Punctidae, the Australian fauna is dominated by charopid taxa. Our analysis showed that the Tasmanian charopid fauna includes representatives of Cystopeltidae and the Punctidae + Charopidae clade, but the family-group affinities of the vast majority of Australian taxa have not yet been determined, and the paleobiogeographic history of the Australian punctoid fauna is not known. Similarly, the family-group affinities and paleobiogeographic histories of charopid taxa from Africa, New Caledonia and Saint Helena, are not known.

In summary, some extant punctoid genera are interpreted as having stratigraphic ranges extending back to the lower Neogene or middle Paleogene, and fossil assemblages from South America, New Zealand and Oceania also include extinct punctoid genera (e.g., Solem 1977; Miquel and Rodríguez 2015; Marshall and Worthy 2017). The fossil record in South America indicates that Cystopeltidae, Punctidae in the restricted sense and 'Charopidae' existed as separate family-level groups by Eocene time, and thus must have diverged sometime prior to that. The oldest known fossils of Endodontidae are Early Miocene in age, but the basal position of this family in Punctoidea suggests that it diverged from the lineages giving rise to Cystopeltidae and the Punctidae + Charopidae clade in the Paleocene or earlier. The oldest known fossils assigned to Punctidae and Charopinae are of Late Oligocene and Early Miocene age, respectively (Wenz 1923; Pierce 1992; Marshall and Worthy 2017), indicating that these groups had diverged by the Late Paleogene. By Early Miocene time the Punctidae had attained a very wide distribution, with at least two genus groups in New Zealand (*Atactolaoma*, *Paralaoma*), and species of *Punctum* in South America, North America and Europe, but the latter genus (and Punctidae in general) evidently subsequently became extinct in South America. The basal group of Punctidae in our phylogenetic analysis contains the New Zealand genera *Laoma* and *Phrixgnathus*. These

two genera are not known from any pre-Quaternary fossil assemblages in New Zealand or elsewhere, but must have diverged from the group of *Paralaoma* and *Punctum* in the Oligocene or earlier. The shells of *Laoma* and *Phrixgnathus* typically have a color pattern of radial stripes and zigzags, whereas shells of *Paralaoma* and *Punctum* are generally smaller and uniformly brown in color. Whether the *Laoma-Phrixgnathus* lineage originated in the New Zealand region in the Paleogene, or dispersed there from elsewhere later in the Cenozoic, is not known.

From a morphological and evolutionary perspective it is interesting to note that, although the vast majority of punctoid taxa have coiled external shells that animals can fully retract into, shell reduction leading to limacization has occurred independently in the endemic Australian genus *Cystopelta* (Cystopeltidae), and in separate lineages within the Punctidae + Charopidae clade, including the endemic New Zealand genera *Ranfurlya* (Charopinae) and *Otoconcha* (Otoconchinae). The phylogenetic relationships of *Flammoconcha* Dell, 1952, another endemic New Zealand genus of punctoid semi-slugs, have not yet been determined. There are, however, no known cases of limacization within Endodontidae, which might have been precluded by aspects of their pallial anatomy (Solem, 1976).

Conclusion

Based on our results, we propose the following revised taxonomic classification.

Superfamily Discoidea Thiele, 1931 (1866)
Family Discidae Thiele, 1931 (1866)
Family Oreohelicidae Pilsbry, 1939
Superfamily Punctoidea Morse, 1864
Family Endodontidae Pilsbry, 1895
Family Cystopeltidae Cockerell, 1891
Family Punctidae Morse, 1864
Family Charopidae Hutton, 1884
Helicina *incertae sedis*
Family Helicodiscidae Pilsbry, 1927

The North American genus *Radiodomus* Baker, 1930 is transferred from Charopidae and treated here as *incertae sedis* within Discoidea. In Punctoidea, family Cystopeltidae has been expanded to include not only the type genus *Cystopelta*, but also some other Australian and South American genera. Whether or not any charopid genus groups from Africa, New Zealand, New Caledonia and Oceania also belong in Cystopeltidae has not yet been determined. Charopidae is provisionally retained as a family-level name for a paraphyletic group of taxa, pending further study of phylogenetic relationships within Punctoidea. The relationships of Helicodiscidae within Helicina remain uncertain, but it is an independent branch that is separate from both Punctoidea and Discoidea.

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Supplementary material 1

Species identification and stylommatophoran phylogeny

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Data type: species data

Explanation note: The supplement contains: (1) further information regarding species identification; and (2) a large-scale molecular phylogeny of Stylommatophora, made to test the polyphyly of Punctoidea.

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